NEW TAXA OF FOSSIL BIRDS

Pierce Brodkorb

The taxa of fossil birds proposed below are published in advance of future parts of the Catalogue of Fossil Birds, so that the names may be used in forthcoming works of other authors.

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Hovacrex, new genus

Type *Tribonyx roberti* Andrews (1897, p. 356, pl. 9, figs. 4-7). Related to *Tribonyx* DuBus, but pelvis with posterior renal depression wider, preacetabular ilium without depression above pectineal process; tibiotarsus with internal condyle more massive, extensor bridge less oblique, intercondylar groove wider and shallower, shaft wider, and fibular crest relatively long. Name formed from *Hova*, the dominant tribe of Madagascar, and *crex*, Greek, feminine, a rail. Only included species *Hovacrex roberti* (Andrews), Quaternary, Sirabé, Madagascar. Family Rallidae.

Idiornithidae, new family

Type *Idiornis* Oberholser (1899, p. 202). Gaillard (1908, p. 113) set up *Orthocnemus* and *Elaphrocnemus* Milne-Edwards (1891, pp. 74, 77) under the vernacular name "famille des Orthocnémides," for which Lambrecht (1933, p. 490) proposed the family Orthocnemidae. As *Orthocnemus* is a preoccupied senior synonym of *Idiornis*, the family name must be altered accordingly. The group is known from the Lower Eocene or Upper Oligocene phosphorite du Quercy, France. Suborder Ralli.

Neanis, new genus

Type *Hebe schucherti* Shufeldt (1913, p. 644). Name from Greek, *neanis*, feminine, a maiden. As *Hebe* was preoccupied in 1826 by Risso, a new name is required. Only included species *Neanis scucherti* (Shufeldt), Lower Eocene, Green River Formation, Wyoming. Tentatively referred to the family Scytalopidae [synonyms Pteroptochidae, Rhinocryptidae].

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ECOLOGY OF THE INDIGO BUNTING IN FLORIDA

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Since the settlement of North America by Europeans, some major biotic communities such as the temperate deciduous forest have been drastically altered by agricultural and lumbering practices. Much of the original forest has been replaced by cultivated fields and forest edge communities, and ecologists are familiar with increases and decreases of animal populations as the result of modifying the climax community structure. Indeed, the marked population decline of bird species, such as the ivory-billed woodpecker (*Campephilus principalis*) and Bachman's warbler (*Vermivora bachmanii*), has been attributed to the destruction of their preferred habitat. On the other hand, disturbance of the climax community can result in the proliferation of other habitats and niches when secondary successional stages become more widespread. In the southeastern United States early seral stages and sub-climax stages may support a more varied avifauna and denser populations of birds than the climax community (Odum, 1950; Johnston and Odum, 1956).

Over its entire range in North America, the indigo bunting (*Passerina cyanea*) is typically a species of the forest edge, abandoned weedy fields, roadsides, and shrubby ravines (Taber and Johnston, in press). When closed stands of forest in the eastern United States are cleared and secondary succession takes place, this bunting would be expected to increase in numbers in its preferred habitats. Increases during recent years have been reported for northwestern Florida (Sprunt, 1954), Ohio (Trautman, 1940), and Maryland (Warbach, 1958). Wells (1958, pp. 223-4) ably traced historical aspects of the increase of this species: "Perhaps originally a bird of successional vegetation within the Eastern Deciduous Forest of North America, and of the oak openings along the prairie-forest ecotone, the Indigo Bunting was undoubtedly restricted in numbers by the relatively closed canopy of the climax forest. . . . In the east the opening of the forest canopy by agriculture, logging, and burning, and in the western grasslands the planting of trees, coupled with cessation of burning, converted great areas into potential Bunting habitat. This species has apparently responded to these changes with a great increase in population and extension of range. . . . "

Agricultural practices have radically altered some of the landscape of north-central Florida over the past few decades, a result being the replacement of the once extensive pine and hardwood forests by pastureland and agricultural fields. Increasing pastureland acreage has been associated with the northward spread of the burrowing owl (*Speotyto cunicularia;* Ligon, 1963). As some pastures and other fields are abandoned, especially those on small farms and around towns, the stage is set for secondary succession and potential bunting habitat. The purpose of this paper is to trace the recent increase of indigo buntings in Florida and to point out aspects of its ecology in the state.

Distribution

When Sprunt revised *Florida Bird Life* in 1954, the indigo bunting was regarded as an uncommon transient, occasional in winter, and an uncommon breeding bird in the northern part of the state. Actual breeding records were limited to a single nest at Gainesville, numerous accounts from northern Leon County, and probable nesting in the Fort Walton area. Since that time Henry M. Stevenson has informed me (personal communication) of the scattered occurrence of this species in the summers between 1960 and 1964 in the following additional counties: Pasco, Hillsborough, Suwannee, Columbia, Taylor, and Dixie. Although at these sites no nests were found, the widespread occurrence of singing males in the summer is strong circumstantial evidence for breeding.

For the Gainesville region Chapman (1888) had only a single record (January 27, 1887); it was not listed by Baynard (1913); Howell (1932) gave a single March 15 record for Lake City; and McClanahan (1935, 1937) added several fall records for Gainesville. Before 1964 there was only one known breeding record for Gainesville—H. H. Bailey (1925) reported a nest with young on July 17 and 18. In 1964, territorial singing males were observed at ten different locations in Alachua, Gilchrist, and Levy counties (Fig. 1). At most of these sites only one to three males were noted, but near Fannin Springs (site number 9 on Fig. 1), William Colson and I counted at least 11 singing males on a 77-acre tract on July 25, 1964. Similiar numbers were observed at this site on succeeding days. Several of these males were caught in nets and banded, several females were seen, and three nests were located. Two nests contained two eggs each and another nest contained three partially fledged young.

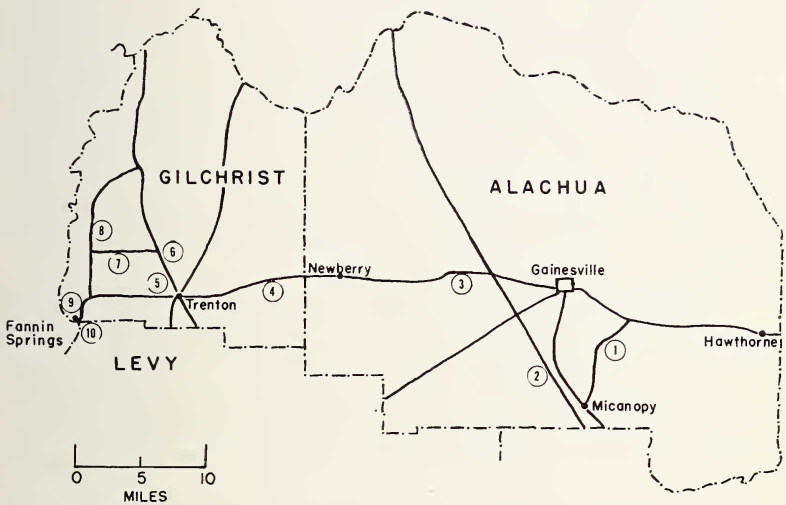


Fig. 1. Breeding sites of the indigo bunting in three counties of north-central Florida, summer of 1964.

Habitats utilized by the territorial buntings of north-central Florida generally fall into two categories—young pine plantings with open expanses of tall grasses and forbs, and abandoned fields grown up in scattered shrubs and low trees. The latter habitat is essentially "grassland-shrubland," the conventional ecological term for describing this stage in upland plant succession (Johnston and Odum, 1956). Both of these habitats in north Florida are ecologically similar to the species' preferred habitats over the entire breeding range in eastern North America. They provide the ecological requirements for a successful breeding season, e.g. singing perches, open areas for feeding, cover for nesting and protection. An interesting man-made habitat had been created at the Fannin Spring site where the greatest concentration of buntings was recorded. In 1962 about 80 acres of mesic hammock were partially cleared of dense undergrowth for a proposed housing subdivision, but in the clearing process numerous scattered oaks 30-40 feet high were left. Because the subdivision plans failed, the entire area, criss-crossed with roads, became subject to natural secondary succession. As a result, by 1964 the open upperstory of oaks had a sparse understory of sumach, grape, dog fennel, palmetto, and young oaks. The understory was open enough so that it could be penetrated with relative ease. In addition to the taller trees, there was a network of power lines used by the male buntings for singing perches.

A large abandoned field of about 100 acres near Paynes Prairie (site number 2 on Fig. 1) supported three pairs of indigo buntings in 1964. This field contained a wealth of scattered young pines (4-10 ft. high) and broad areas of broomsedge and bladder-pod. Two male buntings collected from this field, though on territory and evidently mated, proved to be subadult birds, so identified by plumage characteristics (Dwight, 1900).

During migration in Florida the indigo bunting may occur in habitats similar to the breeding ones, but especially in the autumn these birds are denizens of brushy fields and their edges. In 1963 and 1964 indigo buntings were common from the end of August until early November in some small fields with thick ground cover on the University of Florida campus at Gainesville. The vegetation, consisting of Johnson grass, beggarlice, millet, and corn, was six feet in height. It was in this field that nearly 100 buntings were caught in nets, weighed, banded, and released (Fig. 2).

BREEDING POPULATIONS

Breeding censuses throughout the eastern United States show that the indigo bunting averages about 14 pairs/100 acres in its preferred habitats (Taber and Johnston, in press). For a relatively large area censused, one of the densest populations was 13 pr/25 acres in a Maryland apple orchard (Stewart and Robbins, 1958), and on a small area of tung oil trees north of Tallahassee Herbert L. Stoddard, Sr. (personal communication) recorded 1 pr/2-3 acres. Sprunt (1954) quotes Shannon that near Ft. Walton there may be "as many as '10 singing males to the mile'." The greatest concentration of breeding buntings in the present study was that of the Fannin Spring site where there were at least 11 pr/77 acres during the summer of 1964. The observations of Stevenson cited above for other parts of the state indicated only widely scattered birds and no concentrations.

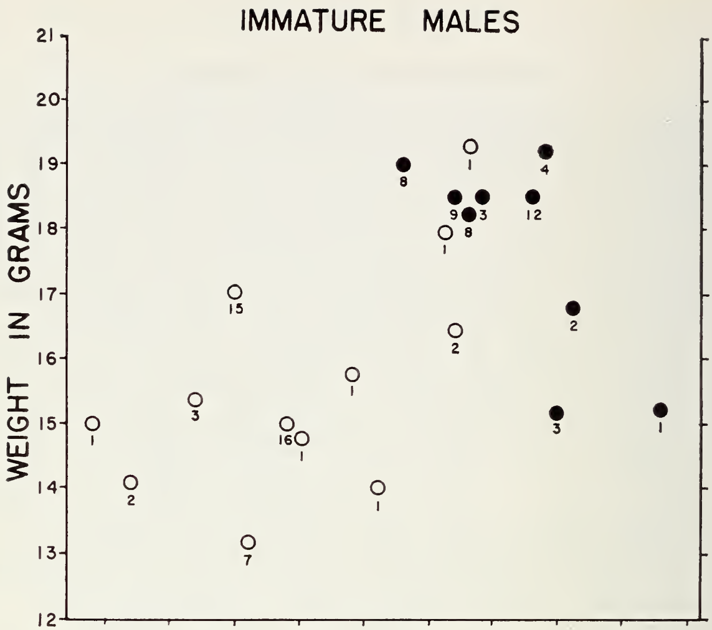
MORPHOMETRIC CONSIDERATIONS

Because of pronounced color differences the bluish adult and second-year male buntings can be easily distinguished from the brown females. The sexes of first-year birds, however, are more difficult to distinguish, even though males in their first autumn tend to have a bluish tinge to the otherwise brown wing coverts and bases of the retrices, whereas the first-year females generally lack this bluish tinge (Dwight, 1900). Using color differences alone, one can separate the sexes of about 90 per cent of first-year birds held in the hand in the autumn. Another useful measurement in birds is that of the wing chord. Accordingly, for all the first-year birds caught at Gainesville, wing lengths in millimeters were as follows: for 53 ♂♂, mean ± S. E. = 63.6 ± 0.25 mm., range = 59.4-66.6; for 24 ♀♀, mean ± S. E. = 62.0 ± 0.39, range = 59.6-63.4. These data for wing lengths are significantly different at the 5 per cent level. Furthermore, on any given day in the fall the first-year males tend to be heavier than the females (Fig. 2).

Thus, first-year males tend to be more bluish, to have longer wings, and to be heavier than first-year females at this time of year.

MIGRATION ROUTES AND ESTIMATED FLIGHT RANGES

For years there has been controversy among some ornithologists as to whether migrating birds fly over or around the Gulf of Mexico from Florida and other Gulf Coast states. As regards this bunting, the evidence now supports use of both routes (Cooke, 1911; Stevenson, 1957) the bulk of the population in spring likely pursuing a trans-Gulf route. Fat studies of migratory birds killed at a television tower near Tallahassee convinced Odum and his colleagues (Odum, 1960) that only a small percentage of the buntings in autumn had enough fat to fly nonstop across the Gulf. The alternative circum-Gulf route was suggested. However, at that time it was not known that there is evidently a major autumnal flight of indigo buntings down peninsular Florida, a flight indicated by significant numbers caught at Gainesville. Most of these migrants at Gainesville were immature birds; evidently adults migrate earlier than the time when the samples were obtained or use a different route. These migrating individuals could have moved toward the west coast, then pursued a circum-Gulf route, but I suspect that a sizable proportion of them "island-hop" to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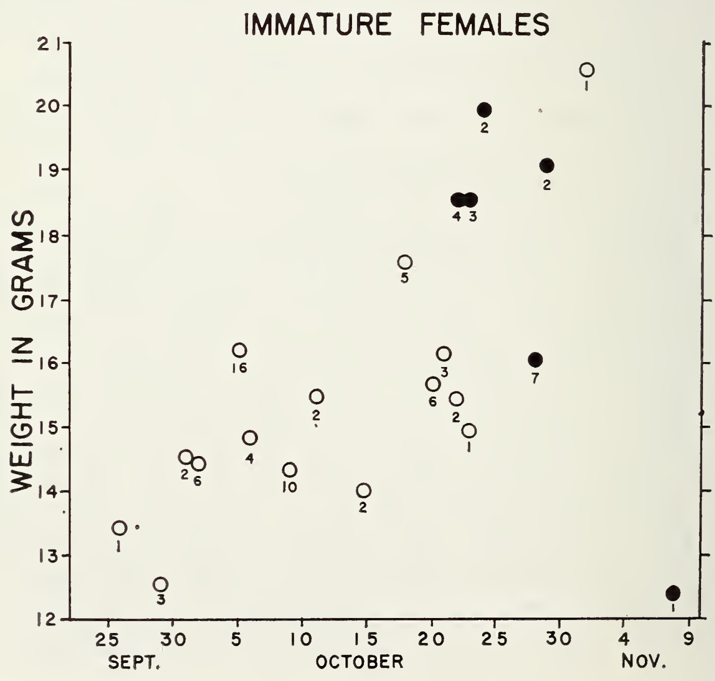
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overwinter in the Greater Antilles or remain in southern Florida for the winter.

Migratory birds are generally leanest during or immediately following the breeding season. From Table 1 it is instructive to note the weights of breeding adult males from North Carolina; their average weight was 13.8 g. The extensive chemical analyses of Connell et al. (1960), have shown the average fat-free weight of indigo buntings to be 13.1 g for 37 males and 12.5 g for 18 females. Putting these two sets of data together we can postulate that the breeding males in North Carolina had about 0.7 g of fat. Although this is only an average figure, it is reasonably close to the value of 1 g of "reserve fat" that some investigators have claimed for a species of this size.

By knowing the average fat-free weight for this species, can we now predict the fat content of a live bird if its body weight is known? In other words, as an individual gains weight during the migratory period, is the increase in weight due to increments in water, body mass (protein and carbohydrate), fat, or some combination of the three? Evidence from the detailed investigations on white-crowned sparrows (*Zonotrichia leucophrys*) by Donald S. Farner and his students indicates that increase in weight is not accompanied by an increase in water content. Furthermore, for several other species of migrating birds Odum et al. (1964, p. 1037) clearly demonstrated that there is no "appreciable change in the water content or the nonfat dry weight of the body as a whole." Thus, gains in body weight by small migrant birds, such as the indigo bunting, before or during migration should be due to fat increments alone.

Odum (1960) calculated that an indigo bunting would require about 30 per cent of its body weight in fat before it could fly non-stop across the Gulf of Mexico from northern Florida, a distance of about 600 miles. He went on to suggest for his indigo bunting sample that (p. 573) " . . . only about six individuals out of the sample of 55 . . . would have been able to continue non-stop across the Gulf; most individuals would have had to follow the land route or else stop along the coast for extensive re-fueling before attempt-

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Fig. 2. Average weights of immature (first-year) indigo buntings in autumn. Open circles represent birds killed at a television tower near Tallahassee, Florida; closed circles are for birds caught at Gainesville. Figures below symbols indicate numbers of specimens.

TABLE 1

Body weights of indigo buntings

Locality	Date	Males		Females	
		Adults	Immatures	Adults	Immatures
Winston-Salem, North Carolina	June 5-20, 1963 (June 18*)	13.8 (12.5-14.8) n = 8			
Middle South Carolina (Norris and Johnston, 1958)	June 26-Aug. 28 (Aug. 12)	13.3 (12.6-14.0) n = 2			14.0 (13.0-14.0) n = 2
Gainesville, Florida	Sept. 8-Sept. 21, 1964 (Sept. 16)	14.6 n = 1	13.8 (12.9-15.5) n = 13	14.0 n = 1	13.2 (12.3-15.4) n = 10
Middle South Carolina (Norris, R. A., unpublished data)	Sept. 24-Oct. 16, 1957 (Oct. 5)	16.9 (15.2-19.2) n = 7	16.5 (14.7-19.4) n = 5	14.8 (14.4-15.1) n = 5	16.3 (14.0-18.7) n = 5
Northwest Florida (Connell et al., 1960)	Sept. 24-Nov. 1 (Oct. 6)	15.4 (12.9-19.6) n = 17	15.5 (12.9-21.2) n = 53	15.9 (13.3-21.4) n = 13	15.4 (11.9-22.2) n = 60
Middle Georgia (Johnston and Haines, 1957)	Oct. 8, 1954 (Oct. 8)	15.9 (13.9-17.3) n = 17	17.5 (15.8-19.1) n = 3	15.7 (12.7-18.7) n = 8	17.2 (14.0-19.0) n = 5
Gainesville, Florida	Oct. 18-Nov. 8, 1963 (Oct. 23)		18.3 (12.6-26.0) n = 50		17.5 (11.8-22.0) n= 24

* Median date of specimens collected.

ing the over-water flight." I have obtained from Dr. Odum the raw weight and fat data for these 55 birds and find that those six individuals weighed 18 or more grams (Fig. 2) and had 32.4-40.0 per cent of their body weight in fat. The actual fat weights ranged from 5.2-8.3 g.

TABLE 2

Estimated flight distances of indigo buntings

Body weight	Fat available	Energy available	Flight distances
14 g	1 g	9.5 kcal	142 miles
15	2	19.0	286
16	3	28.5	428
17	4	38.0	570
18	5	47.5	712
19	6	57.0	864
20	7	66.5	1006
21	8	76.0	1148
22	9	85.5	1290
23	10	95.0	1332
24	11	104.5	1474
25	12	114.0	1616
26	13	123.5	1758

By comparing these figures with the 1963 sample weighed at Gainesville (Table 1), several features become apparent. The males at Gainesville weighed on the average about three grams more than those reported from northwest Florida and the females, about two grams more. If the increased weight were due to fat increments alone, then the Gainesville males had about 5.2 g of fat and the females 5.0 g. Furthermore, if an indigo bunting requires at least 30 per cent of its body weight in fat for a trans-Gulf flight, then the Gainesville males would have had 5.5 g of fat and the females 5.3, on the average. The two values are indeed quite close, one based upon a proposed percentage of body weight in fat and the other based upon an increased weight from fat deposits. In the Gainesville sample out of 74 birds weighed, 43 (59 per cent) had weights of 18 or more grams. On this basis at least these 43 could have flown nonstop across the Gulf. Also from Table 1, the later the time of sampling, generally the heavier (and probably fatter) the buntings become. Had Odum's sample from the Tallahassee tower been extended some two weeks, very likely the birds would have weighed more.

What about those individuals weighing less than 18 g or having less than 30 per cent of the body weight in fat? As Odum indicated, some could have pursued a circum-Gulf route to wintering grounds in Central America. However, the geographical position of Gainesville allows possible alternative routes. Some of the birds, especially the very lean ones, would very likely overwinter in Florida, as there are many winter records especially from south Florida, but even as far north as Gainesville. The very lean female taken on November 8 (Fig. 2) at Gainesville had been previously caught on October 28. Because this particular bird had lingered in the area for a period of time, it appears likely that she would have overwintered there. Other migrating individuals undoubtedly follow a land and sea route to Cuba and Jamaica. In the latter country the species is known to overwinter in moderate numbers.

Several quantitative or semi-quantitative methods have been proposed for estimating flight ranges in small migrant birds. One of these methods depends upon the assumption that the flight rate of energy expenditure is 2, 3, or 4 times the existence rate. For a bird the size of a lean (13 g) indigo bunting Kendeigh suggested an existence rate of 0.64 kcal/hr. Let us now deal with a 18 g bunting, one that contains about 5 g fat that can be catabolized for flight energy. This bird would therefore have 47.5 kcal of available energy. It is known from Cooke's (1937) report that the flight speed of this species is 20 mph. We then arrive at the following figures: if flight energy expenditure is 2 × existence rate, an 18 g bird could fly 688 miles and a 19 g bird, 826 miles. If flight energy expenditure is 3 × existence rate, flight ranges would be, respectively, 490 and 588 miles. These figures suggest that the ratio between flight energy expenditure and existence energy expenditure is between 2 and 3 because the trans-Gulf distance from northern Florida is about 600 miles. These data also reinforce the proposal mentioned above that only a bunting weighing at least 18 g could fly nonstop across the Gulf.

The recent reports by Lasiewski et al. (1964) and LeFebvre (1964) suggest a better quantitative procedure for determining flight distances. According to the graphs depicted by Lasiewski et al. (p. 215), the basal rate of metabolism of a 13 g bird (indigo bunting size) is equivalent to approximately 0.25 kcal/hr. However, by utilizing the formula given by King and Farner (1961)

$$\log M = \log 80.1 + 0.659 \log W \pm 0.076, \text{ or}$$
$$M \text{ (cal/g-hr)} = 35.0\, W^{-0.34}$$

we find that the basal rate of metabolism should be 0.19 kcal/hr for a 13 g bunting. Both Lasiewski (1963) and LeFebvre (1964) have shown that flight energy expenditure is at least seven times the basal rate. Thus, an indigo bunting with a fat-free weight of 13 g would require 1.33 kcal/hr. in flight. By knowing the flight speed we can obtain flight distances as seen in Table 2. Again, it can be seen that only an indigo bunting weighing at least 18 g could fly nonstop the 600 miles across the Gulf of Mexico from northern Florida.

SUMMARY

Observations of breeding indigo buntings in north-central Florida in 1964 indicated not only widespread breeding but also some locally dense populations previously unknown from this portion of the state. The increased occurrences are correlated with an increase in secondary plant succession, this being occasioned by small-scale abandonment of pastures and other cleared areas.

The discovery of concentrations of autumnal migrant buntings at Gainesville afforded the opportunity to obtain valuable morphometric data. Weight data when coupled with flight energy expenditures strongly support the thesis that only buntings weighing at least 18 g could fly nonstop across the Gulf of Mexico to their wintering grounds in Central America. The likelihood of buntings migrating down peninsular Florida and thence to Caribbean islands is also discussed.

ACKNOWLEDGMENTS

It was only through the tireless efforts and careful observations of William Colson, a lifelong resident of Gilchrist County, Florida, that the numerous records near Fannin Springs were obtained. Additional records were called to my attention by Robert Ackerman and Dr. Henry M. Stevenson. Dr. Robert A. Norris kindly supplied some unpublished weight data from South Carolina. These investigations were supported by a grant (GB-2114) from the National Science Foundation.